Organization of Chemically Activated Food Search Behavior in *Procambarus clarkii* Girard and *Orconectes rusticus* Girard Crayfishes

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Abstract. The feeding responses of decapod crustaceans to chemical stimuli have most often been evaluated in terms of one defining act, ignoring the organization of the behavior. To gain greater insight into foraging behavior, we considered the organization of food-search behavior in evaluating the responses of two species of crayfishes to a feeding stimulant. We also examined the effects of food deprivation on the behavioral organization and whether a behavioral dichotomy exists between food search and feeding behavior in these species.

Individual crayfish of the species *Procambarus clarkii* and *Orconectes rusticus* were presented with infusions of a feeding stimulant consisting of a supernatant leachate of 100 ml water and 1 g of fish flakes. The stimulant was injected with a syringe and small-bore plastic infusion tubing into the center of a behavioral arena 25 cm square and 15 cm deep. Total injection time was 20 s. Experimental groups were presented with either the full-strength leachate (100%) or one of five dilutions: 75%, 50%, 25%, 10%, or 0% (controls) of full-strength. The feeding stimulant was presented either the day after the crayfish were fed or after one week of food deprivation. We analyzed three components of food-search behavior—detection, probing (near-field search), and locomotion (far-field, or distant, search)—recording the order of occurrence and the latency time to initiation for each behavior.

When presented with the stimulus following regular feeding, both species responded to concentrations ≥50% full-strength with probing behavior (near-field search) prior to locomotion, and to concentrations <50% full-strength with locomotion prior to, or even in the absence of, probing. Detection always occurred first. These results indicate that chemical stimuli preferentially activate distant food search in both species and that a behavioral dichotomy exists between food search and feeding behavior. One week of food deprivation had no effect on the organization of food-search behavior in *P. clarkii;* however, groups of unfed *O. rusticus* presented with 25% and 10% full-strength concentrations probed prior to locomotion, indicating a change in behavioral organization.

Introduction

Most animals must forage efficiently to optimize both growth and survival (Werner and Mittelbach, 1981; Zimmer-Faust, 1987). An animal that can, from a distance, sense the quality and quantity of food and estimate the effort required to capture it has an advantage. This is especially true in low-light benthic environments because such an ability reduces the time spent choosing food, maximizing the net rate of energy or nutrient gain (*e.g.,* Hughs, 1979; Erichsen *et al.,* 1980; Orians, 1981; Peckarsky, 1984; Zimmer-Faust, 1987).

Many studies have demonstrated that chemical stimuli elicit food-search behavior in decapod crustaceans, often in the absence of other sensory cues (*e.g.,* McLeese, 1970, 1973; Shelton and Mackie, 1971; Mackie, 1973; Hindley, 1975; Derby and Atema, 1982, 1988; Rittschof, 1982; Tierney and Atema, 1986, 1988; Hazlett, 1994; Wilman *et al.,* 1994). In laboratory experiments, visual and tactile prey stimuli are often ineffective, whereas prey odors elicit food-search behavior (*e.g.,* Schembri, 1981; Derby and Atema, 1982; Zimmer-Faust and Case, 1982; Tierney and Atema, 1988; Hazlett, 1994; Wilman *et al.,* 1994). However, crayfish may require experience and learning to associate a particular odor with food (Hazlett, 1994). Foragers are influenced by food-specific chemical stimuli that are essen-

tial for activating and orienting food search (Bell and Tobin, 1982; Tierney and Atema, 1988; Momot, 1995).

Chemical stimuli can influence decapod crustacean foraging by activating far-field (distant) food searching preferentially (*e.g.*, Hazlett, 1971a, b; McLeese, 1973; Atema, 1977; Pearson *et al.*, 1979; Reeder and Ache, 1980). In this behavioral model, chemical concentration may be important in relating distance to food: dilute concentrations of food odor may be interpreted as originating from distant food sources. This model assumes that locomotion (far-field food search) is the primary response to low-concentration chemical stimuli, and that appetitive feeding (near-field search, indicated by probing the substrate) is the primary response to high-concentration chemical stimuli, resulting in a behavioral dichotomy between food search and feeding (Atema, 1977).

An alternative model has been developed from studies on marine crustaceans. Evidence from experiments on many species of marine decapods indicates that response to chemical stimuli activates near-field (nearby) rather than distant food search, regardless of the concentration of the chemical stimuli. Low concentrations of food odor activate substrate probing (appetitive feeding), and only higher concentrations active locomotion. Food search is thus primarily organized to obtain nearby food items, implying that there is no behavioral dichotomy between food search and feeding (*e.g.*, Zimmer-Faust and Case, 1982, 1983; Zimmer-Faust *et al.*, 1984; Zimmer-Faust, 1987; see review, Zimmer-Faust and Case, 1982).

Crustacean feeding responses are often evaluated in terms of one specific defining act in response to a chemical stimulus (*e.g.*, Zimmer-Faust and Case, 1982; Johnson and Atema, 1986; Tierney and Atema, 1988), or to several unrelated behavioral acts (Wilman *et al.*, 1994). These methods of categorizing behavior simplify data collection, analysis, and interpretation, but ignore the structural organization of behavior (Zimmer-Faust and Case, 1982). Greater insight into an animal's foraging behavior may be gained through studying the structural organization of food search (Zimmer-Faust and Case, 1982, 1983; Zimmer-Faust *et al.*, 1984; Zimmer-Faust, 1987).

Wilman *et al.*, (1994) examined the responses of three *Orconectes* congeners to the odor of fish carrion and live predaceous fish (as food). They found that *Orconectes rusticus* Girard is more responsive than either *O. propinquus* Girard or *O. virilis* Hagen to these food odors and speculated that such differential chemoreception is contributing to the success of *O. rusticus* in its invasion of northern Wisconsin lakes, where it is replacing the other two species. Differential chemoreception toward food odors should also be important across genera in species invasions. *Procambarus clarkii* Girard is an exotic invader in nearby Ohio and is replacing *O. rusticus* in certain areas of its range (Norrocky, 1983). If *P. clarkii* is more responsive than *O. rusticus* to food odors, then *P. clarkii* may be able to locate

food more quickly and increase its feeding rate compared to *O. rusticus.*

We quantitatively investigated the organization of food-search behavior in the crayfishes *P. clarkii* and *O. rusticus.* The objectives of our study were to (1) evaluate the sequence of food-search behavior in both species; (2) determine the effects of food deprivation on the organization of food search and feeding in these crayfishes; (3) determine whether a behavioral dichotomy exists between their food search and feeding behavior; and (4) examine the comparative responsives of both species to the feeding stimulant.

Materials and Methods

Experimental animals and maintenance conditions

Ninety-six adult, intermolt, Form II (nonbreeding) crayfish of each species were used in the experiments. All crayfish were >6 cm in total length from rostrum to tail (caudal edge of telson). *Procambarus clarkii* was commercially raised and was obtained from Waubun Laboratories (Schriever, LA). *Orconectes rusticus* was captured from local streams in Erie County, Pennsylvania. Crayfish were held in 25-liter species-specific community aquaria (23° ± 1°C) for at least one week prior to experimentation. Each aquarium contained an average of four to six crayfish, a gravel bottom, a filter, aeration, and sufficient cover material to provide each individual with shelter. A window in the laboratory provided natural photoperiod. Crayfish were fed TetraMin fish flakes, *ad libitum*, daily; they were not fed during experiments. Water was changed in the aquaria weekly. All animals were tested for their behavioral responses to chemical feeding stimuli within 2 weeks after the initial 1-week adjustment period.

Experimental procedures

The 96 crayfish of each species were divided randomly into two experimental series (48 crayfish of each species in each experimental series) of six treatment groups (*n* = 8 per group) per series. They were placed individually into opaque, white plastic behavioral arenas measuring 25 × 25 × 15 cm (length, width, depth) to examine their responses to one of six chemical conditions. Gravel covered the bottom of each arena to a depth of 2.5 cm, displacing 800 ml. Thus each arena held 8.5 liters of laboratory water (tap water treated with NovAqua to remove chlorine and heavy metals).

No crayfish was tested more than once. Both sexes were used in all experiments, with the exception of ovigerous females. Responding to food odor is a basic behavior; there was no *a priori* reason to suspect that male and female crayfish might differ in their responses.

After placement into the arena, the crayfish were given 1 h to adjust to it. For our bioassay, it was essential that the animals were inactive when the chemical feeding stimulant

was infused into the arena. All animals were inactive after this 1-h adjustment period; none had to be removed from the study.

For each trial, an individual crayfish was presented with an infusion of 10 ml of a freshly prepared solution of a chemical feeding stimulant (food odor) or with 10 ml of laboratory water (controls). The stock solution of feeding stimulant consisted of a leachate of 100 ml of laboratory water and 1 g of TetraMin fish flakes. The water and fish flakes were mixed for 5 min in a 250-ml beaker. The supernatant leachate was then poured off into a second beaker. A previous study by Steele *et al.* (1992) demonstrated that this leachate formulation elicits an unambiguous feeding response by crayfish of both species used in the present study.

The 10 ml of leachate was injected by hand into the center of the arena within 20 s (injection rate, 0.5 ml s^{-1}) using a 10-ml hypodermic syringe and small-bore plastic infusion tubing. The infusion tubing was buried beneath the gravel in the arena. It curved upwards to the vertical in the center of the arena, with the end just below the gravel surface. Dye studies indicated that injected chemicals diffused through an arena within 45 s from the beginning of infusion.

Following the adjustment period, the animals in the treatment groups of both species were presented either with the undiluted leachate, full-strength concentration (100%), or with one of five other concentrations: 75%, 50%, 25%, 10%, or 0% (controls) of full-strength. Concentrations were of injected leachate prior to dilution in the arena water. Controls served as indicators of spontaneous detection responses to water flow from injections (rheotaxis) and spontaneous probing and locomotion in the absence of chemical cues. Crayfish were presented with these chemical infusions either the day following regular feeding (Experimental Series I) or after one week of food deprivation (Experimental Series II). All experiments were conducted between 0800 and 1600 h from 14 August through 3 October 1996.

A Sony Hi8 video camera (Model CCD-V701) was mounted above the arena and each animal's behavior was videotaped during each trial. Videotaping began 1 min prior to chemical infusion and continued for 5 min after the end of the infusion. Three components of food-search behavior were analyzed from the videotapes: detection, probing, and locomotion (Itagaki and Thorpe, 1981; Zimmer-Faust and Case, 1982; Zimmer-Faust *et al.*, 1984; Tierny and Atema, 1986). These behaviors are defined in Table I. For each behavior, the numbers of crayfish engaging in it, its rank order of occurrence, and the latency to its initiation (to the nearest 0.1 s) were recorded for each trial. For those groups in which probing preceded locomotion, the total time (to nearest 0.1 s) each crayfish spent probing the gravel was calculated from the initiation of probing to the initiation of locomotion.

Statistical analyses

A *G* test for independence, with Williams' correction for 2 × 2 contingency tables (Sokal and Rohlf, 1981), was used in analyzing the number of crayfish responding to a food-odor concentration compared to laboratory water controls. Because responses to the five food-odor concentrations were compared to the control results, we used a significance level of 0.01 for each comparison to achieve a maximum experimentwise error of 0.05. The Mann-Whitney *U* test (Sokal and Rohlf, 1981; Rohlf and Sokal, 1981) was used to compare behavioral response times following regular feeding and after food deprivation between the same treatment concentrations between species, and to compare the times of initiation of each behavior and the total times spent probing for each concentration of chemical feeding stimulant following regular feeding between the species. The Kruskal-Wallis one-way rank ANOVA (Rohlf and Sokal, 1981; Sokal and Rohlf, 1981) was used to compare behavioral response times following regular feeding and after food deprivation among treatment concentrations within a spe-

Table I

Definitions of behavioral elements in crayfish food-search behavior

Behavior	Definition
Detection behavior	
Lower antennule	Antennules directed downward or held parallel to the body.
Near-field search	
Leg probing	Any non-locomotor movement of a pereiopod (ambulatory leg) which rakes a dactyl across the substratum, inserts it into the substratum, or elevates it above the substratum.
Chela probing	Any non-locomotor movement of the first pereiopod which rakes a chela across the substratum, inserts it into the substratum, or elevates it above the substratum.
Digging	Leg probing and chela probing.
Far-field search	
Walking	Lateral or anterior movement of the body a distance greater than one carapace length.
Climbing	Cephalothorax angled above the substratum, with at least four walking legs not in contact with the substratum.
Locomotion	Gross body movement (walking and climbing).

cies, and to compare the times of initiation of each behavior and the total times spent probing for each concentration of chemical feeding stimulant following regular feeding with the responses following food deprivation within each species. Where the Kruskal-Wallis analysis indicated significance in the data, a nonparametric multiple comparison test based on the Student-Newman-Keuls (SNK) test was used for all pairwise comparisons (Glantz, 1997).

Results

Numbers responding to chemical stimuli

Except for the detection component, the responses of both fed and food deprived *P. clarkii* to food odors $\geq 25\%$ full-strength are significantly greater ($P < 0.01$, at least) than the responses of the controls to laboratory water (Table II). In most instances where significant differences occurred, all individuals in the experimental groups exhibited a response to the food odors. Of the control individuals, both fed and food-deprived, half or fewer exhibited detection or locomotion behaviors, and none exhibited probing, in response to injections of laboratory water (Table II).

Both fed and food-deprived *O. rusticus* responded to food odors $\geq 25\%$ full-strength in significantly greater numbers than the controls responded to laboratory water (Table II). In all instances where significant differences occurred, all individuals in the experimental groups exhibited a response to the food odors (Table II). Fewer *O. rusticus* controls responded than did *P. clarkii* controls; as with *P. clarkii*, *O. rusticus* controls responded with detection or locomotion behaviors, none with probing (Table II).

Types of responses to chemical stimuli—regularly fed groups

For all regularly fed individuals of both *P. clarkii* and *O. rusticus*, concentrations $\geq 50\%$ full-strength of the chemical feeding stimulant induced first detection, then probing (defined as near-field search), and lastly, locomotion (defined as far-field search) (Table III). In contrast, concentrations $<50\%$ full-strength induced first detection, then locomotion prior to—or even in the absence of—probing in those individuals responding (Table III). Initiation of locomotion in both species at stimulant concentrations $\geq 50\%$ full-strength was delayed considerably by intensive probing, compared to experimental groups receiving $<50\%$ full-strength injections of feeding stimulant (Table IV).

The time to initiate a food-search behavior following the start of odor injection was compared across stimulant concentrations for each species and between species for similar stimulant concentrations. The results of Kruskal-Wallis and Mann-Whitney U tests for all comparisons are summarized here, and in Table IV.

Within species. For *P. clarkii*, response times were significantly different with respect to detection, probing, and locomotion for stimulant concentrations $\geq 50\%$ full-strength compared with lesser concentrations. The results of Kruskal-Wallis analyses indicated significant differences in the times of detection ($H_{corrected} = 30.252$; $P < 0.001$), probing ($H_{corrected} = 28.317$; $P < 0.001$), and locomotion ($H_{corrected} = 32.029$; $P < 0.001$) among the experimental groups receiving the different stimulant concentrations. Results of the nonparamentric comparisons indicated that responses at 100%, 75%, and 50% full-strength were not

Table II

Behavioral responses (numbers of crayfish responding) of P. clarkii *and* O. rusticus *to chemical feeding stimuli following regular feeding and food deprivation*

Food odor conc. (% full-strength)	Regular Feeding			Food Deprivation		
	Detection	Probing	Locomotion	Detection	Probing	Locomotion
Procambarus clarkii						
100	8	8***	8*	8	8***	8*
75	8	8***	8*	8	8***	8*
50	8	8***	8*	8	8***	8*
25	8	8***	8*	8	8***	8*
10	4	4	4	8	8***	8*
0	4	0	2	3	0	2
Orconectes rusticus						
100	8**	8***	8**	8*	8***	8*
75	8**	8***	8**	8*	8***	8*
50	8**	8***	8**	8*	8***	8*
25	8**	8***	8**	8*	8***	8*
10	6	5	5	5	5	5
0	1	0	1	2	0	2

Responses that are significant compared to controls (*G*-test with Williams' Correction) are marked with asterisks: * $P < 0.01$; ** $P < 0.005$; *** $P < 0.001$. All others are not significant ($P > 0.01$).

Table III

Ranked order of initiation (1st, 2nd, 3rd) of behaviors after chemical stimulus infusion for Procambarus clarkii *and* Orconectes rusticus *crayfish following regular feeding and following one week's food deprivation*

Food odor conc. (% full-strength)	Behavior	Following regular feeding						Following food deprivation					
		P. clarkii			O. rusticus			P. clarkii			O. rusticus		
		1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd
100	Detection	8	0	0	8	0	0	8	0	0	8	0	0
	Probing	0	8	0	0	8	0	0	8	0	0	8	0
	Locomotion	0	0	8	0	0	8	0	0	8	0	0	8
75	Detection	8	0	0	8	0	0	8	0	0	8	0	0
	Probing	0	8	0	0	8	0	0	8	0	0	8	0
	Locomotion	0	0	8	0	0	8	0	0	8	0	0	8
50	Detection	8	0	0	8	0	0	8	0	0	8	0	0
	Probing	0	8	0	0	8	0	0	8	0	0	8	0
	Locomotion	0	0	8	0	0	8	0	0	8	0	0	8
25	Detection	8	0	0	8	0	0	8	0	0	8	0	0
	Probing	0	0	8	0	0	8	0	0	8	0	0	8
	Locomotion	0	8	0	0	8	0	0	8	0	0	8	0
10	Detection	4	0	0	6	0	0	4	0	0	5	0	0
	Probing	0	0	4	0	0	5	0	0	4	0	5	0
	Locomotion	0	4	0	0	5	0	0	4	0	0	0	5
0 (Controls)	Detection	4	0	0	1	0	0	3	0	0	2	0	0
	Probing	0	0	0	0	0	0	0	0	0	0	0	0
	Locomotion	0	2	0	0	1	0	0	2	0	0	2	0

significantly different from each other ($\alpha > 0.05$), but were significantly different from responses at 25% and 10% full-strength (which were not significantly different from each other; $\alpha > 0.05$) for detection, ($\alpha = 0.05$), probing ($\alpha = 0.01$), and locomotion ($\alpha = 0.05$).

Although the pattern of response latency was slightly different for *O. rusticus* across stimulant concentrations, there was, in general, also a significant difference in the response times for each behavior at stimulant concentrations ≥50% full-strength compared to responses at concentrations <50% full strength. Kruskal-Wallis analyses indicated significant differences in the times of initiation of detection ($H_{corrected} = 32.699$; $P < 0.001$), probing ($H_{corrected} = 35.077$; $P < 0.001$), and locomotion ($H_{corrected} = 28.189$; $P < 0.001$) among the experimental groups receiving the different stimulant concentrations. Nonparametric comparisons indicated that for detection and probing, responses at 100% full-strength were significantly different from re-

Table IV

Comparisons of mean initiation time(s) of behavior after chemical stimulus injection for Procambarus clarkii *and* Orconectes rusticus *crayfish following regular feeding*

Food odor conc. (% of full-strength)	Detection			Probing			Locomotion		
	P. clarkii	O. rusticus	P-value	P. clarkii	O. rusticus	P-value	P. clarkii	O. rusticus	P-value
100	11.7	14.0	NS	15.7	17.0	NS	148.3	31.2	***
	(4.62)	(4.62)		(5.03)	(5.06)		(20.72)	(4.54)	
	11.3	20.0	***	15.7	30.5	**	136.7	45.4	**
	(1.53)	(0.90)		(3.06)	(9.37)		(13.80)	(10.16)	
50	9.5	19.6	**	16.3	23.9	*	108.0	36.9	**
	(3.50)	(3.81)		(6.81)	(2.95)		(13.46)	(2.66)	
25	25.0	28.4	NS	46.9	50.8	NS	31.8	32.3	NS
	(5.97)	(6.37)		(7.51)	(3.22)		(7.31)	(7.10)	
10	34.6	48.6	NS	50.8	68.8	NS	43.6	55.9	NS
	(9.90)	(8.71)		(7.07)	(9.20)		(2.83)	(3.05)	

Times are measured from start of odor infusion. Standard deviation is given in parentheses. Significance levels for Mann-Whitney *U* tests comparing responses between species: * $P < 0.05$; ** $P < 0.025$; *** $P < 0.001$; NS, not significant ($P > 0.05$).

Table V

Comparisons of mean initiation time(s) of behavior after chemical stimulus infusion for Procambarus clarkii and Orconectes rusticus crayfish following one week's food deprivation

Food odor conc. (% of full-strength)	Detection			Probing			Locomotion		
	P. clarkii	O. rusticus	P-value	P. clarkii	O. rusticus	P-value	P. clarkii	O. rusticus	P-value
100	11.6	17.4	*	13.0	22.3	**	120.0	33.8	**
	(1.70)	(6.68)		(1.56)	(5.50)		(9.90)	(8.42)	
75	10.0	21.8	*	12.8	30.8	*	137.1	41.3	*
	(2.83)	(2.31)		(5.23)	(2.08)		(10.21)	(2.52)	
50	12.6	24.5	***	14.8	31.2	***	117.2	44.1	***
	(4.57)	(2.60)		(5.24)	(1.04)		(18.40)	(3.50)	
25	22.9	26.1	NS	37.8	29.4	NC	29.2	39.7	NC
	(10.2)	(1.62)		(12.2)	(1.47)		(9.66)	(5.78)	
10	41.3	51.9	*	58.1	55.7	NC	52.5	69.4	NC
	(11.20)	(3.96)		(18.70)	(1.72)		(17.71)	(8.62)	

Times are measured from start of odor infusion. Standard deviation is given in parentheses. Significance levels for Mann-Whitney U tests comparing responses between species: * $P < 0.05$; ** $P < 0.025$; *** $P < 0.001$; NS, not significant ($P > 0.05$); NC, Not Calculated, since these responses had different ranked orders of occurrence following food deprivation.

sponses at all other concentrations of leachate ($\alpha = 0.05$), and responses at 75% and 50% full-strength were not significantly different from each other ($\alpha > 0.05$) but were significantly different ($\alpha = 0.05$) from responses at 25% and 10% full-strength (which were not significantly different from each other; $\alpha > 0.05$). For locomotion, responses at 100%, 75%, 50%, and 25% full-strength were not significantly different from one another, but were significantly different ($\alpha = 0.05$) from responses at 10% full-strength.

Between species. In seven out of nine comparisons between *P. clarkii* and *O. rusticus* at stimulant concentrations ≥50% full-strength, the responses were significantly different (Mann-Whitney U test, $P < 0.05–0.01$; Table IV). Except for responses to 100% full-strength stimulant, *P. clarkii* detected the feeding stimulant and began probing the gravel significantly sooner than did *O. rusticus.* Locomotion in *P. clarkii* was significantly delayed compared to *O. rusticus* due to the increased amount of time *P. clarkii* spent probing the gravel (mean ± SD: 132.6 ± 42.41 s at 100%; 121 ± 14.11 s at 75%; 91.7 ± 29.26 s at 50% full-strength) compared with *O. rusticus* (mean ± SD: 14.2 ± 2.92 s at 100%; 14.9 ± 0.95 s at 75%; 13.0 ± 0.61 s at 50% full-strength). Results of Mann-Whitney U tests were significant for all comparisons at $P < 0.01$ (Table IV). At stimulant concentrations <50% full-strength, there were no significant differences in any behavioral responses between the species (Mann-Whitney U tests, $P > 0.05$; Table IV).

Types of responses to chemical stimuli–food-deprived groups

One week of food deprivation had no effect on the organization of food search in *P. clarkii* (Table III). As with the regularly fed groups, concentrations ≥50% full-strength of the chemical feeding stimulant induced first detection,

then probing and, lastly, locomotion. Concentrations <50% full-strength induced first detection and then locomotion prior to probing in those individuals responding.

In *O. rusticus,* however, one week of food deprivation altered the organization of food search for those groups presented with 25% and 10% full-strength concentrations of the feeding stimulant (Table III). As with their conspecifics presented with greater concentrations, they now initiated probing (near-field search) prior to locomotion.

The times of initiation of food-search behaviors after stimulus injection following one week of food deprivation were compared between species at similar concentrations and within species for all concentrations. The results of Kruskal-Wallis and Mann-Whitney U tests are summarized here and in Table V.

Within species. For food-deprived *P. clarkii,* the patterns of latency for detection, probing, and locomotion for all odor concentrations were no different from those of the regularly fed groups, with significant latency differences at concentrations <50% full-strength (compare Tables IV and V). The results of Kruskal-Wallis analyses indicated significant differences in the times of initiation of detection ($H_{corrected} = 30.427$; $P < 0.001$), probing ($H_{corrected} = 29.155$; $P < 0.001$), and locomotion ($H_{corrected} = 29.674$; $P < 0.001$) among the experimental groups receiving the different stimulant concentrations. Results of the nonparametric comparisons indicated that responses at 100%, 75%, and 50% full-strength were not significantly different from each other ($\alpha < 0.05$), but were significantly different from responses at 25% and 10% full-strength (which were not significantly different from each other; $\alpha > 0.05$) for detection, ($\alpha = 0.01$), probing ($\alpha = 0.01$), and locomotion ($\alpha = 0.05$).

Food-deprived *O. rusticus* displayed fewer differences in

latencies for the initiation of food-search behaviors than did the regularly fed groups. The only significant time differences were seen at the 10% full-strength concentration (compare Tables IV and V). Kruskal-Wallis analyses indicated significant differences in the times of initiation of detection ($H_{corrected}$ = 22.069; P < 0.001), probing ($H_{corrected}$ = 25.678; P < 0.001), and locomotion ($H_{corrected}$ = 21.377; P < 0.001) among the experimental groups receiving the different stimulant concentrations. Nonparametric comparisons indicated that for detection, probing, and locomotion, responses at 100%, 75%, 50%, and 25% full-strength were not significantly different from one another, but were significantly different (α = 0.05) from responses at 10% full-strength.

Between species. The results of comparisons were similar to those following regular feeding (Table IV), except that now the responses of *P. clarkii* differed significantly from those of *O. rusticus* for every behavior at stimulant concentrations ≥50% full-strength; *P. clarkii* detected the feeding stimulant and probed significantly sooner than did *O. rusticus* (Table V). As in the regularly fed groups, locomotion in *P. clarkii* was significantly delayed compared to *O. rusticus* due to the time spent probing the gravel by *P. clarkii*. At all three stimulant concentrations ≥50% full-strength, *P. clarkii* probed the gravel significantly longer before initiating locomotion (mean ± SD: 107.0 ± 8.34 s at 100%; 124.3 ± 5.23 s at 75%; 102.4 ± 35.06 s at 50% full-strength) than did *O. rusticus* (mean ± SD: 11.5 ± 5.85 s at 100%; 10.5 ± 1.50 s at 75%; 12.9 ± 2.59 s at 50% full-strength) (Mann-Whitney U test, P < 0.01 for all comparisons; Table V). Due to the altered order of initiation of locomotion and probing in *O. rusticus* presented with ≤25% full-strength stimulant (Table III), interspecific comparisons for the initiation times were not calculated. At the 10% full-strength concentration, food-deprived *P. clarkii* detected the stimulus significantly sooner than did food-deprived *O. rusticus* (Table V).

Discussion

As expected, both *Procambarus clarkii* and *Orconectes rusticus* crayfishes responded to the feeding stimulant, suggesting that chemoreception is used in the foraging strategy of both species. The results indicate that low concentrations of chemical feeding stimuli preferentially activated far-field (distant) food search in both species following regular feeding. Appetitive feeding (near-field search, or probing the substrate) always occurred before locomotion (far-field, or distant search) in response to high-concentration stimuli (≥50% full-strength), indicating that a behavioral dichotomy exists between food search and feeding behavior in these species. Detection always occurred first. Thus, there is a linear organization of these behavioral components of food-search behavior.

Our results differ from those of experiments with a variety of marine decapod crustaceans. Those studies indicate that chemical feeding stimuli selectively activate near-field (nearby) rather than distant food search, regardless of the stimulus concentration. In those studies, lesser concentrations of food odor activated substrate probing (appetitive feeding), and only greater concentrations of food odor activated locomotion. Thus, food search in those species is primarily organized to obtain nearby food items, implying that there is no behavioral dichotomy between food search and feeding (*e.g.,* Zimmer-Faust and Case, 1982, 1983; Zimmer-Faust *et al.,* 1984; Zimmer-Faust, 1987; see review in Zimmer-Faust and Case, 1982).

One week of food deprivation had no effect on the organization of food search and feeding in *P. clarkii* for either rank order of occurrence or latency to initiation of any of the components of food-search behavior. One week of food deprivation, however, did affect the organization of food search and feeding in *O. rusticus* for those crayfish presented with 25% and 10% full-strength concentrations. Crayfish in these groups now initiated probing prior to locomotion (a reversal of previous behavior). In natural situations this behavior would appear not to be adaptive given the low probability of finding food nearby. Otherwise, there were no statistically significant effects of food deprivation on the behavioral responses of either species.

Perhaps the behavior of *O. rusticus* presented with the low-concentration feeding stimulants following one week of food deprivation is not as maladaptive as it first appears. It could be that food deprivation has made the animals less selective in their foraging strategy, and that any concentration of food odor is sufficient to initiate appetitive feeding behavior prior to locomotion. Perhaps food deprivation leads individual *O. rusticus* to interpret low-concentration food odors as originating from small nearby food items (*sensu* Reeder and Ache, 1980; Zimmer-Faust and Case, 1982). Under those conditions the behavior might represent an adaptive foraging strategy for this species. In addition, freshwater crayfishes (as well as marine decapods) locomote spontaneously; thus chemical induction of locomotion may not always be necessary for "distant" foraging to occur (Zimmer-Faust and Case, 1983).

For stimulant concentrations of 50% and 75% full-strength, *P. clarkii* detected the feeding stimulant and began probing significantly sooner than *O. rusticus,* both following regular feeding and after food deprivation (see Tables IV and V). The initiation of locomotion in *P. clarkii* was significantly delayed compared to *O. rusticus* due to the time the former spent probing the gravel. At all three stimulant concentrations ≥50% full-strength, *P. clarkii* probed the gravel significantly longer before initiating locomotion than did *O. rusticus* (see Tables IV and V, and Results). *Procambarus clarkii,* therefore, appears to be significantly more responsive to moderate concentrations of food odors, at least in this experimental situation, than does *O. rusticus* for all three behavioral components of food

search behavior. We speculate that such differential chemo-
reception in response to food odors could contribute to the
invasion success of *P. clarkii* by allowing crayfish of this
species to detect economically significant food items more
quickly.

Acknowledgments

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